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MYCOTROPHY: ITS OCCURRENCE AND POSSIBLE SIGNIFICANCE AMONG EPIPHYTIC ORCHIDACEAE[1]

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Orchidaceae and mycotrophy are practically synonymous to many botanists. This impression could be illusory, however, its basis being little more than the long-known symbiotic germination of certain orchid seeds which is thought to be representative of all members of the family (Arditti, 1967, 1979; Warcup, 1975), and the persistence of extensive fungal infections in the root systems of at least a few terrestrial adults. Species native to soil do pass through heterotrophic phases assisted by mycobionts, some lasting years (e.g., *Cypripedium)* or, in exceptional cases where the phytobiont is an achlorophyllous saprophyte or epiparasite (e.g., *Corallorhiza*), a lifetime (Burgeff, 1936, 1959; Harley, 1969).

Broad conclusions about the physiological profiles of mature orchids cannot be extrapolated from any number of studies on juveniles, nor from knowledge of a single group of ecologically similar adults, no matter how complete. Orchidaceae is an immense family of uncommon diversity. Most of its members prefer sites quite deviant from those of the better-studied, temperate terrestrials and doubtless possess specialized nutritional characteristics to match. Thus, while possibly true, Sanford's statement (1974) that "it is remarkable that this (mycorrhizal) relationship is so ancient and even more remarkable that it has not been lost in any of the present-day species, terrestrial or epiphytic" rests largely on conjecture, as do claims that epiphytic orchids use a fungal intermediate to draw nutrients from living hosts (Ruinen, 1953; Furman & Trappe, 1971; Johansson, 1977) and that narrow host preferences expressed by some orchids are obliged by infecting fungi (Johannson, 1974; Jonsson & Nylund, 1979).

Seedlings of most epiphytic orchids, like those of temperate species, reportedly require exogenous sources of fixed carbon for early growth (Arditti, 1967, 1979). Perhaps, as has long been assumed, this commodity is supplied in nature by a mycobiont. On the other hand, carbohydrates or other acceptable carbon sources may exist in sufficient concentrations on wet bark surfaces to induce asymbiotic germination and support subsequent heterotrophic growth, at least briefly (Sanford, 1974). Compared to those of soil dwellers, protocorms of epiphytic species green up quickly, suggesting that an obligate dependence on outside sources of fixed carbon, whatever their origin, is fleeting, or in some instances, even nonexistent. Certainly small propagule size in itself does not mandate mycotrophy -- witness the autotrophic germination of most homosporous pteridophytes -- nor is the capacity of many epiphytes to live out autotrophic lives in doubt (e.g., Bromeliaceae, some of which have little or no root development as adults).

The continuance of a symbiotic fungal association into adult stages of epiphytic orchids is open to even greater question than is its existence in their juveniles. Burgeff (1959) and Ruinen (1953), advocates of mycotrophy among epiphytic taxa, have reported a fungal presence in the roots of certain paleotropical species, but the nutritional significance of this association was not established. A survey by Hadley & Williamson (1972) of canopy-dwelling taxa in Malaysia convinced them that heavily infected roots are not characteristic of mature epiphytes; fungal endophytes, if present at all, were confined to those parts of root systems embedded in moist debris. Many arboreal orchids -- in particular, the very xeric ones (extreme types *sensu* Benzing,

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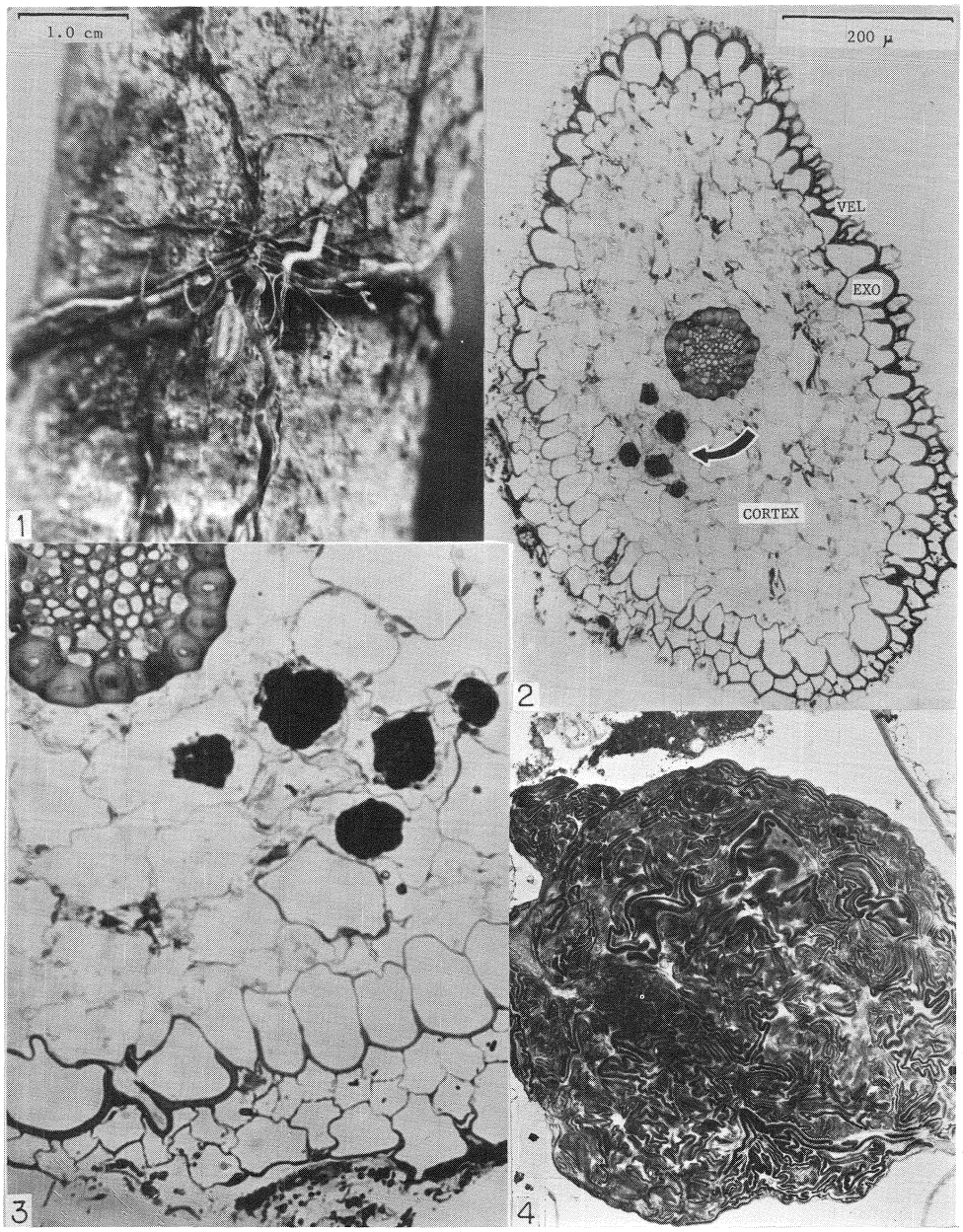

Figure 1. Fruiting specimen of *Harrisella porrecta* growing on *Taxodium ascendens* in the Big Cypress Swamp region of southwestern Florida.
Figure 2. Epon-embedded, 1 μ cross section of *H. porrecta* root collected from the same host -- cortex, exodermis (EXO) and velamen (VEL) tissues are labeled. Dark arrow indicates several pelotons located in cortical cells on the side of the root adjacent to the host.
Figure 3. Same pelotons at higher magnification.
Figure 4. Epon-embedded cross section of single peloton visualized by TEM.

1978) -- grow with their roots clinging to exposed bark surfaces where conditions in the rhizosphere would not seem to be especially conducive to delicate hyphal outgrowths. In no case have fungal inhabitants noted in roots of epiphytic orchids been studied to assess their nutritional competence or nutrient exchanges with phototrophic partners. Orchid-fungus interactions among terrestrials and cultured seedlings of epiphytes range from symbiotic to parasitic, with fungi serving as either hosts or parasites, depending on the taxa involved and conditions of culture (Alconero, 1969; Hadley, 1970; Arditti & Ernst, 1972; Lewis, 1973).

Horticulturists have known for many years that canopy-dwelling orchids are capable of autotrophic growth from very early life stages on through maturity. Nevertheless, given the paucities of available inorganic nutrients in tree crowns and the abundance of complex organic substrates, even a limited and facultative biotrophy could be advantageous to an epiphyte. Fungi shown to associate with orchids are commonly virulent pathogens to other organisms (Lewis, 1975), in part because of their ability to attack such complex organic compounds as lignin and cellulose (Hadley, 1969). This capacity is restrained by infected orchid cells, however, and some of the mycobiont's metabolites are, in fact, uncharacteristically (for mycorrhizal fungi) siphoned off to support the phytobiont (Smith, 1966; Purves & Hadley, 1975). Orchid mycobionts could conceivably provide substantial nutritional benefits to their associates even if no carbon gain were involved. The enhanced mineral-scavenging capacities of many mycorrhizal soil-rooted plants relative to uninfected members of the same taxa are well established (Harley, 1969; Malloch *et al.*, 1980).

While pursuing studies of orchid root photosynthesis (Benzing & Ott, in press), we discovered clear evidence of mycorrhizal involvement in several mature *Polyradicion lindenii* and *Harrisella porrecta* specimens collected from *Fraxinus caroliniana* and *Taxodium ascendens* hosts in southern Florida. These findings are germane to the controversy concerning the existence of mycotrophy among orchidaceous epiphytes for three reasons: (1) the roots in question had been growing fully exposed on bark surfaces that remain dry for extended periods during the winter months (Figure 1); (2) the shootless condition of these plants (Figures 1, 5) has been cited as evidence of their heterotrophic nutrition, although other explanations for this condition have been offered by Benzing (1979) and Benzing & Ott (in press); and (3) the mycorrhizal association (Figures 2, 3, 4, 7) involves the digestion of hyphal coils, suggesting fungal substrates are being coopted by the orchid.

Fungal development was most extensive in *Polyradicion* (Figure 6). Here, affected cells exhibited clear evidence of long-standing, yet still active, infections in the form of pelotons plus numerous undamaged hyphae (Figure 7). Apparently, both primary and secondary infections were present. Endophytes were confined to that side of the root adjacent to the host (Figure 2). Hyphal extensions through passage cells located in this region (Figure 8) indicate that mycobionts grown beyond the exodermal barrier into the velamen and could then invade host bark tissue. Clearly, the existence of typical orchidaceous mycorrhizas among canopy-dwelling members of the family is unequivocal. The extent of the association and its significance to these organisms remain to be determined. Considering that many aspects of canopy-dwelling orchid biology have already been ascribed to their microbial endophytes, the time to define this relationship on a firm physiological basis is long overdue.

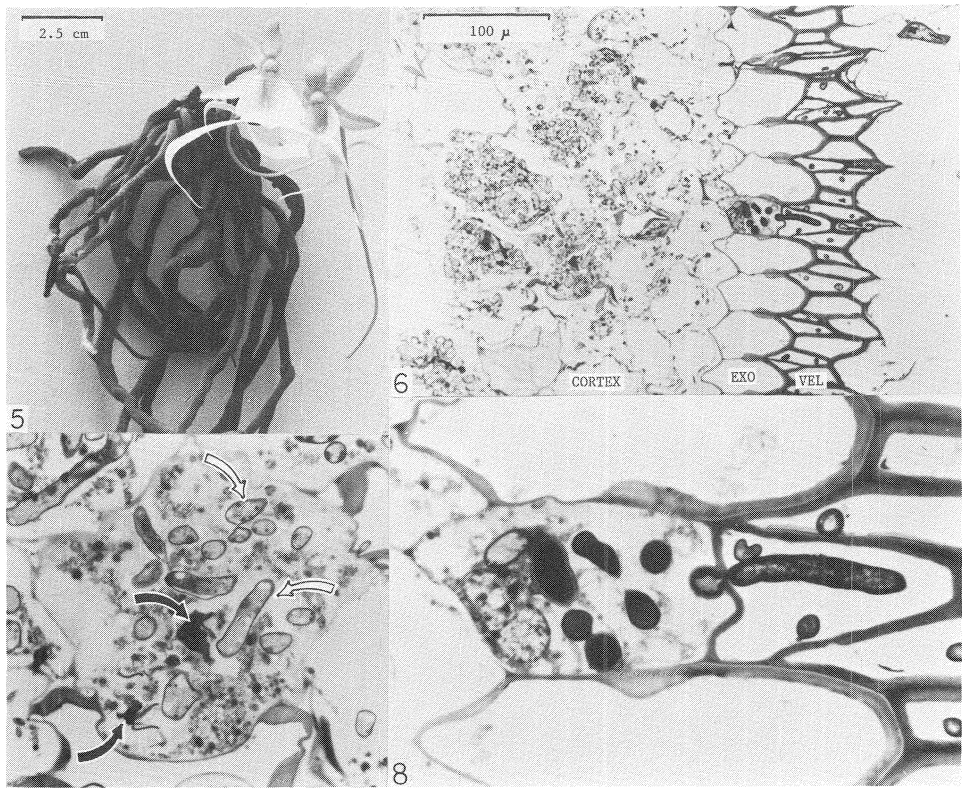

Figure 5. Flowering specimen of *Polyradicion lindenii* grown free of a host in greenhouse culture.

Figure 6. Epon-embedded 1 μ cross section of *P. lindenii* root which was collected on *Fraxinus caroliniana* in the Fahkahatchee Slough regions of southwestern Florida. Cortex, exodermis and velamen tissues are indicated. Note the heavy fungal infection of many cortical cells adjacent to the host.

Figure 7. Individual cortical cell of *P. lindenii* root featured in Figure 6 containing small pelotons (black arrows) and undamaged hyphae (open arrows).

Figure 8. Living passage cell in exodermis seen in Figure 6 containing hyphae. Note hypha penetrating the outer tangential wall of passage cell from the velamen. A number of additional hyphae can be seen in the otherwise empty velamen cells.

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